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A FUNCTIONAL ANALYSIS OF JAW MECHANICS IN THE DINOSAUR *TRICERATOPS*

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INTRODUCTION

The many species of ceratopsian or horned dinosaurs were characterized by several peculiar and conspicuous features: 1) very large heads, 2) great bony "neck shields," 3) strong, laterally compressed, turtle-like beaks, 4) unique shearing dentitions of great power, and 5) prominent brow or nasal horns—the latter absent in very primitive ceratopsians. These structures, as shown by Lull (1933) and Colbert (1948), dominated ceratopsian evolutionary trends. All but the last of these characters were either part of, or were directly involved with, the feeding apparatus. Thus, ceratopsian evolution appears to have been dominated by progressive structural modification of the feeding mechanism.

The present paper is part of a more extensive investigation of the significance of mandibular mechanics in ceratopsian evolution. The purpose of this paper is to present a functional analysis of ceratopsian mandibular mechanics and mastication as they are

reflected in *Triceratops*, the last and most common ceratopsian genus. The several components of the masticating apparatus, including the dentition, musculature and those skeletal structures directly involved, are reconstructed and described, and a mechanical analysis of the mandibular lever is presented for five species of *Triceratops*.

MATERIALS AND METHODS

The skulls and jaws of seven specimens of *Triceratops* were selected without regard to species assignment on the basis of quality and completeness of preservation of the pertinent structures. Although any other advanced ceratopsian would have served as well, *Triceratops* was selected simply because of the greater availability of good material, *Triceratops* specimens being far more abundant in existing paleontologic collections than are specimens of any other advanced ceratopsian. Linear measurements were made with a steel tape, or with calipers where practicable, to the nearest quarter centimeter. Angular measurements were made directly from the specimens with a large protractor nine inches in radius. All measurements were taken at least twice and where possible these were checked against dimensions of the opposite side. In most instances, only slight differences were noted in dimensions of opposite sides, major discrepancies occurring only where crushing or incomplete preservation obscured original dimensions.

The materials used in this study are housed in the paleontologic collections of the following institutions, the names of which are abbreviated as follows:

AMNH—The American Museum of Natural History.

USNM—United States National Museum.

YPM—Peabody Museum of Natural History, Yale University.

Specimens included in this analysis are:

Triceratops brevicornus, YPM No. 1834

Triceratops elatus, AMNH No. 5116

Triceratops elatus, USNM No. 2100

Triceratops flabellatus, YPM No. 1821

Triceratops prorsus, YPM No. 1822

Triceratops serratus, AMNH No. 907

Triceratops serratus, YPM No. 1823

MASTICATING APPARATUS

Dentition.—The dentition of *Triceratops*, like that of all other advanced ceratopsians, is highly specialized and not at all comparable to that of any other vertebrate, although there are superficial resemblances to the grinding dentitions of the contemporaneous hadrosaurs. Teeth are arranged in long, solid and tightly compacted magazines or batteries deeply implanted in the dentary and maxilla. These batteries, approximating 50 per cent of the total mandibular length, consist of from fifteen to thirty-five closely packed, vertical columns of functional and replacement teeth, each column or series being capped by a single functional tooth (see Figs. 1 and 2).

Individual teeth of *Triceratops* have a slightly curved, wedge-shaped crown, which is enameled on one side only (lingual side in lower teeth and labial side in upper teeth), and a broad, double-fanged root that straddles the succeeding replacement tooth (see Fig. 2). The enameled face is marked by a prominent keel or ridge that extends vertically over the full height of the crown. This keeled, triangular crown face curves transversely across the long tooth axis so that the thin enamel layer of any functional tooth is transected by the steep occlusal surface (see Figs. 2 and 3).

The number of replacement teeth in a particular vertical series is dependent on the position of that series within the battery, those series near battery mid-length consisting of the greatest number

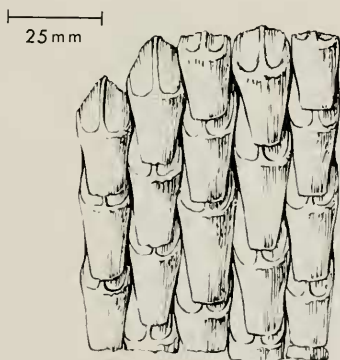


Fig. 1. A segment of the right mandibular battery of *Triceratops brevicornus* (YPM No. 1834), in medial view, showing the arrangement of functional teeth and the underlying non-functional replacement teeth. The lingual wall of the dentary has been removed to expose the dental battery.

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(four or five) while series near either end of the battery may contain as few as two teeth. In lingual aspect (Fig. 1) these tooth columns are straight and nearly vertical, but in transverse section (Figs. 2 and 3) the mandibular series curve up and outward, while the maxillary series curve down and inward.

As reported by Edmund (1960), tooth replacement in ceratopsians is typically reptilian, with the eruption of functional teeth occurring sequentially in alternate vertical series and progressing in wave-like fashion from back to front. Thus adjacent vertical series are nearly one half cycle out of phase and a given functional tooth is erupted slightly more than one half crown height higher than the functional tooth immediately in front. Consequently, the lingual aspect of an exposed mandibular battery of *Triceratops* (Fig. 1) presents a rhombic mosaic of closely packed teeth, not unlike the rhombic pattern of hadrosaurian dental batteries. Unlike the latter, however, there is never more than one functional tooth in each vertical series of the ceratopsian battery. This is because the plane of occlusion is nearly parallel to the axial plane of the dental magazine in higher ceratopsians, whereas there is a signifi-

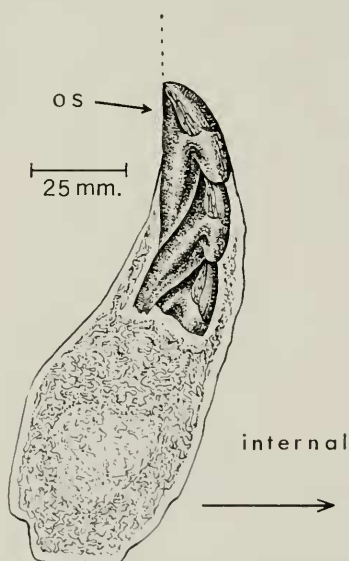


Fig. 2. Transverse section at mid-battery through the left mandible of *Triceratops brevicornus* (YPM No. 1834). Notice the vertical orientation of the occlusal surface (O.S.) and the succession of replacement teeth.

cant angle of intersection (usually at least 30°) between the occlusal plane and the axial plane of the hadrosaurian battery.

Dental Occlusion.—The most critical feature of ceratopsian dentitions is the manner of occlusion. With the exception of *Protoceratops* and the apparently aberrant *Leptoceratops*, occlusion in all members of the Ceratopsia was exclusively one of shear. Crushing or grinding was not possible in any of the known higher ceratopsians. Figure 2, a transverse section through the lower jaw and dentition of *Triceratops brevicornus* (YPM no. 1834), shows the relationship of the occlusal plane to the mandibular battery. It is apparent in this illustration that the surface of wear is nearly vertical, parallel to the plane of mandibular adduction, and that no grinding or crushing component existed. Examination of the occlusal surfaces in any of the other higher ceratopsians reveals them to be exactly the same; nearly straight antero-posteriorly and vertical in orientation, extending continuously over the full length of both mandibular and maxillary batteries. The occlusal surface of the lower dentition extends along the labial side of the battery (the side lacking enamel), and that of the upper battery along the lingual side (see Fig. 3). Notice that the unilateral distribution of enamel on opposite sides of upper and lower teeth, together with the respective curvature of crown faces, and the vertical occlusal surfaces, places the resistant enamel at the most critical site—the cutting edges of each of the opposing batteries. Notice also that the keels of the enameled crowns produce strongly “serrated” cutting edges over the full length of these batteries. The worn dental surfaces conclusively establish the manner of occlusion and mastication in *Triceratops*.

The dentition of these creatures functioned exclusively as cutting structures with the mandibular batteries shearing up inside of the maxillary batteries precisely in the manner of two pairs of adjacent shears.

The occlusal surfaces of two specimens examined (*Triceratops serratus*, AMNH No. 907 and YPM No. 1823) are so straight longitudinally and so nearly vertical that the scissors analogy made above is no exaggeration. Most specimens, however, show varying degrees of warp in the occlusal surfaces, so that the total worn surface of a particular battery may not be absolutely planar or

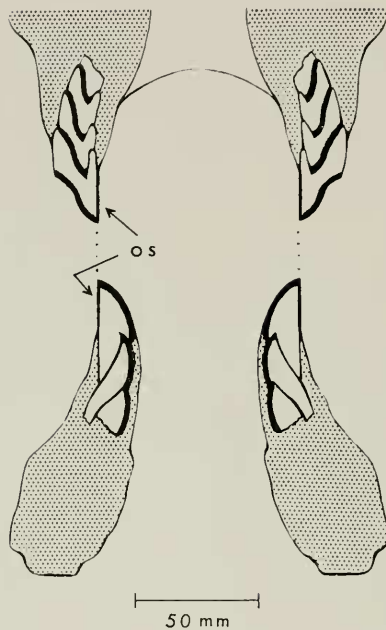


Fig 3. Diagrammatic transverse section of the upper and lower jaws and dental batteries of *Triceratops brevicornus* (based on YPM No. 1834), showing the occlusal surfaces (O.S.), manner of occlusion, and the pattern of tooth succession. The heavy dark lines indicate the position of the enamel. Notice the strategic location and the oblique transection of these enamel plates.

perfectly vertical at every point. These irregularities are natural in part, but in many instances they are the result of post-mortem distortion and crushing. Even where natural, however, such irregularities are minor and do not lessen the significance of the peculiar and specialized nature of ceratopsian occlusion.

While a shearing occlusion is not unusual, it is commonly associated with a carnivorous mode of life. Ceratopsians, however, have repeatedly been judged as herbivores. Limited dental shear is characteristic of numerous herbivores, both mammalian and saurian (artiodactyls, perissodactyls, rodents, multituberculates, tritylodonts, diadectids, turtles, etc.) but in each of these, shearing capacities are associated with, and usually overshadowed by, grinding or crushing capabilities. Apparently, shear is of only minor or secondary importance in most herbivorous species. Thus it is par-

ticularly significant that virtually all known ceratopsian dentitions were specialized shearing dentitions totally devoid of any crushing or grinding properties.

It must be emphasized at this point that the shearing action described here is not a new interpretation. It was first noted by Hatcher (p. 46) and Lull (p. 193) in their monograph on the ceratopsian dinosaurs (Hatcher, Marsh and Lull, 1907) and was referred to subsequently by Lull (1908), Tait and Brown (1928) and Russell (1935). These authors gave brief consideration to this dental specialization and to possible diets and modes of life. But, in my opinion, the full significance of this peculiar dental adaptation has not been fully explored. If the dominant and unique anatomical structure in ceratopsian evolutionary trends (the parietosquamosal frill or "neck shield") was indeed an extended platform for the attachment of enlarged mandibular muscles, as suggested by Lull (1908) and later by Russell (1935) and Haas (1955), is it not possible—in fact, is it not probable—that this unique structure was correlated with the unusual manner of dental occlusion and mastication in ceratopsians?

Mandibles.—The mandible of *Triceratops* is heavy and robust, forming a solid foundation for the large mandibular battery (see Figs. 4 and 5). It is composed of five bones (dentary, splenial, angular, surangular and articular) and articulates rostrally with a sixth, unpaired, median element (prementary). The dentary is by far the largest bone, constituting more than 70 per cent of the lower jaw length. Rostrally it is laterally compressed but deep and meets the opposite dentary in a long, shallow and rather weak symphyseal suture. This junction, however, is strengthened by the overlapping and "enclosing" articulation of the deeply excavated, beak-like prementary.

Posteriorly, the width of the dentary increases very rapidly so its posterior width is about four times its anterior width. This transverse thickening at the rear of the lower jaw (see Fig. 5) results from a pronounced lateral expansion of the dentary that forms the broad base of a high and very stout coronoid process. Aside from the dentition, this prominent coronoid process is the most critical and revealing structure of the lower jaw. Unlike the usual vertebrate coronoid process that rises from the dorsal surface

of the dentary behind the dentition, that of *Triceratops* (and all other higher ceratopsians) extends out and upward from the lateral surface of the dentary, well below the dental battery and far lateral to the plane of occlusion. This process rises well above the mandibular dentition as a massive, laterally convex shaft. Its summit is usually rugose and strongly expanded antero-posteriorly. The location, height, massive construction, and expanded, rugose summit all point to a very prominent role for this structure in mandibular mechanics.

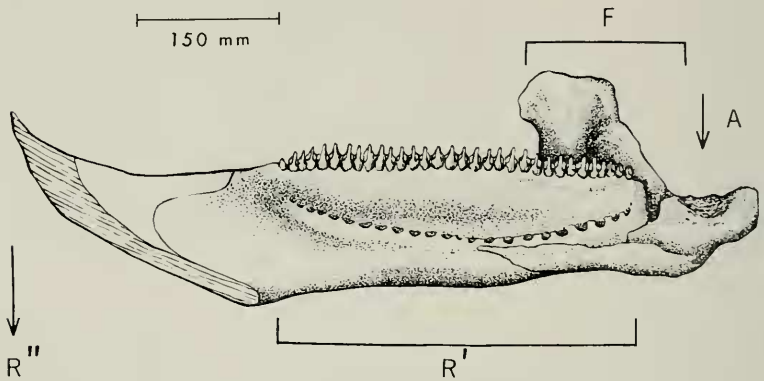


Fig. 4. Right mandible of *Triceratops brevicornus* (YPM No. 1834) in medial view, showing the relative positions of the dental battery with its continuous serrated shearing edge, the coronoid process, and the glenoid facet. Abbreviations: A, mid-point of the glenoid articulation (fulcrum); F, zone of muscular attachment (force application); R' location of resistance (food at the dentition); R'', extreme rostral position of resistance (food between the beaks).

Directly beneath the base of the coronoid process, immediately anterior to the glenoid facet, is the deep Meckelian fossa opening dorso-caudally toward the quadrate. This cavity is bordered by the dentary laterally, dorsally and medially, by the splenial ventromedially and by the angular, surangular and articular posteriorly.

The posterior end of the mandible is composed of three bones—the angular ventrally, the surangular laterally, and the articular dorsally. The surangular, largest of the three, forms a strong posterior buttress at the base of the coronoid process, extending dorsally in some specimens almost to the crest of that process. The surangular also contributes to the anterior part of

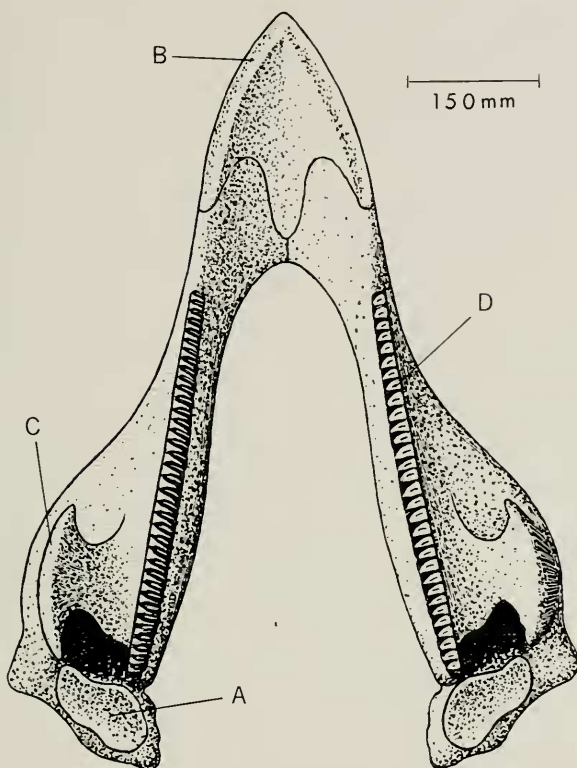


Fig. 5. Mandibles of *Triceratops brevicornus* (YPM No. 1834) in dorsal aspect showing the massive construction of the rear half of the jaws, the large glenoid facet (A), the scoop-like beak (B), the stout coronoid process (C), and the dental batteries (D). Note the anterior convergence of left and right dental batteries.

the glenoid, but the major part of that surface is formed by the articular. The angular underlies and articulates with both the surangular and articular, forming the ventral surface of the caudal extremity of the lower jaw. Although none of these bones are large or massive, they are firmly united by strong sutural contacts to form a solid unit for articulation with the suspensorium of the skull.

The articular facet or glenoid is a prominent, but shallow, broad, obliquely transverse groove situated immediately behind the Meckelian fossa and the posterior extremity of the mandibular battery (see Fig. 5). Although slightly irregular and gently concave, this articular facet has a distinct inclination, facing dorso-

caudally (parallel to the axis of the quadrate and toward the parietosquamosal frill) instead of directly upward. It is this inclined attitude of the glenoid surface that reflects the direction of greatest stress at the jaw joint — viz., rostro-ventral. This substantiates a point to be made later, that the resultant or composite line of action of the mandibular adductors was dorso-caudally oriented. Although not of primary importance, the inclination of the glenoid also clearly precludes any significant retraction of the mandibles, just as the rostral convergence of the dentition prevents any mandibular protraction. Notice that the jaw articulation is placed well below the mandibular dentition (see Fig. 4).

The lower dentition, situated entirely within the dentary in the posterior portion of the jaw, extends from just in front of the glenoid to a point anterior to the midpoint of the mandible. Its length is approximately half the total mandibular length, the anterior portion of the lower jaw, including the beak, being edentulous. As noted elsewhere, a critical character of the lower jaw and its dentition is the fact that the dental magazine extends well behind the coronoid process to a point very close to the jaw articulation. Thus, a significant fraction of the dentition lies posterior (and medial) to the coronoid process.

Cranial Structures.—The skull of *Triceratops* is well known, those of several species having been described and illustrated in earlier publications (see Hatcher, Marsh and Lull, 1907 and Lull 1933). For this reason, a detailed description will not be presented here. However, it is necessary to point out several cranial features that are directly related to mastication and jaw mechanics.

The maxilla, as the foundation for the large upper battery, is of obvious importance. Like the dentary, it is a massive bone containing a deep, ventrally facing groove for the dental battery extending over most of its length. In lateral aspect, it is sub-triangular in shape with irregular and rugose superior surfaces for firm sutural unions with the adjacent bones of the skull. Although there is little evidence to indicate that these sutures fuse, evidence of strong sutural unions does exist in the fact that the maxillae are rarely separated from adjacent skull elements. Extensive sutural contacts, particularly with the pterygoid, palatine and ectoptery-

goid postero-medially, the jugal and lachrymal postero-laterally and dorsally, and the premaxilla anteriorly resulted in a solid and firm dental platform entirely comparable to that of the mandibles. An unpaired, beak-like rostral bone, articulating with both premaxillae, further strengthened the maxillary foundation. The rostral, the dorsal counterpart of the prementary, is very similar to the latter except that it is much deeper and slightly broader, thereby permitting the prementary to fit up inside of the rostral upon full adduction of the lower jaw.

The suspensorium of *Triceratops* consisted of a very stout quadrate which was heavily reinforced laterally by large jugals and quadratojugals and posteriorly by expanded squamosals. The shaft of the quadrate is very stout, both transversely and longitudinally. It is joined to the pterygoid medially by means of extensive suture, dorsally to the squamosal, and overlapped laterally by the bones of the lower temporal arch. Of particular importance is the orientation of the quadrate, which instead of being perpendicular to the axis of dental occlusion, or leaning forward, as in most reptiles, is inclined caudally at an angle of 30° to 40° to the axis of occlusion, nearly parallel to the principal axis of the frill and normal to the glenoid facet. The distal end of the quadrate has the form of a slightly distorted, transversely oriented cylinder with inflated ends and a moderately restricted center. It is evident from the expanded distal end, the stout quadrate shaft and its inclined attitude, and the buttressing of the quadrate by adjacent bones of the skull that the suspensorium of *Triceratops* was constructed to resist unusually high stresses.

The great "neck shield" is the most conspicuous feature of the skull of *Triceratops*, as it is in virtually all ceratopsians. As early as 1908, this frill was correlated with mastication and interpreted by Lull as an area of origin for powerful jaw muscles. Subsequent studies by Lull (1933), Russell (1935) and Haas (1955) have reinforced this interpretation, although a possible secondary function (protection) has been noted. In all ceratopsians, the frill consists of a great dorso-caudal expansion of the squamosals and parietals, reaching far behind the condyle and completely overlapping the cervical region. Colbert (1948) has plotted the relative lengths of various ceratopsian frills, showing that this structure ranges from about 45 per cent of the total skull length in *Proto-*

ceratops to 66 per cent in *Pentaceratops*. In *Triceratops*, although there is some variation, the frill constitutes about half of the total adult skull length.

Of critical importance to the hypotheses which correlates the ceratopsian "neck shield" with jaw musculature is the proposed muscle passage—the path from the mandible to the dorsal surface of the shield through the supratemporal fenestra. Ceratopsians, being diapsids, are characterized by both lateral and supratemporal fenestrae. In *Triceratops* (and all higher ceratopsians) the lateral fenestra is extremely small, presumably as a consequence of the buttressing of the quadrate by adjacent bones of the lower arch and temporal region. The supratemporal fenestra on the other hand exists as a shallow, but broad, slit-like opening in the anterior region of the frill just behind the brow horns. In all *Triceratops* specimens examined, this passage extends dorso-caudally as an absolutely straight tract from the summit of the adducted coronoid process through the upper temporal opening to the dorsal surface of the frill. A similar, broad, slit-like passage is characteristic of all higher ceratopsians, but in some (*Monoclonius*, *Anchiceratops*, *Pentaceratops*, and *Torosaurus*) the passage is slightly deflected within the supratemporal channel and thus is not perfectly straight.

The topographic evidence preserved on the upper surface of *Triceratops* frills is highly suggestive, but not conclusive, as regards the scars of muscle attachment. For most ceratopsians, surface topography and patterns suggest that the frill was almost entirely covered by large muscle sheets (see Russell, 1935 and Haas, 1955). *Triceratops*, however, shows no such evidence, but instead possesses a relatively large frill which seems to lack distinct scars of muscle attachment, except in the immediate vicinity of the supratemporal fenestra. As a result, Russell (1935) reconstructed the mandibular muscles as attaching in a restricted area around the fenestra and immediately behind it, in marked contrast to the very large posterior muscular extension postulated for *Chasmosaurus* and others. However, a few specimens of *Triceratops* (*T. flabelatus*, YPM No. 1821; *T. hatcheri*, USNM No. 2412; and *T. serratus*, YPM No. 1823) suggest that muscle attachments on the frill may have been more extensive than Russell suggested. It is quite possible that a deeper *pars profundus* of the *M. adductor*

externus was attached by a strong fleshy origin about the borders of the supratemporal fenestra, leaving a distinct scar of origin. This would account for the features preserved in nearly all *Triceratops* frills. A longer pars medialis of the M. adductor externus may have attached by a thin sheet of fascia to the frill margins and left little or no indication of its attachment.

MANDIBULAR MUSCULATURE

Before considering the jaw mechanics of *Triceratops*, it is appropriate for us to examine the probable arrangement of mandibular muscles as they have been reconstructed by various students. Several works over the last half century have reviewed ceratopsian jaw musculature, beginning with that of Lull (1908) and followed by that of Russell (1935) and Haas (1955). Although there are several points on which these authors differ, including terminology, all agree that the ceratopsian frill was primarily concerned with mandibular musculature. Both Lull and Russell maintained that the frill may secondarily have provided protection for the neck region in *Triceratops*, chiefly because of the afore-mentioned indications that the frill in this genus may not have been entirely covered by muscular tissues.

Lull (1908), in what must be regarded as one of the first significant attempts at reconstructing the musculature of an extinct animal, presented a careful analysis of the muscles of mastication in *Triceratops*, relating their possible points of attachment and operation, and drawing an analogy with the modern frilled chameleon. The fact that Lull's reconstruction is chiefly mammalian in character should not detract from the worth of this paper, for with the exception of Dollo's (1884) effort, reconstructions of this type had not been attempted before.

Briefly, Lull pictured 1) a powerful temporal muscle extending from the anterior region of the frill (adjacent to the supratemporal fossa) downward and forward to the posterior margin of the coronoid process, 2) external and internal pterygoid muscles running nearly vertically from the pterygoid to the postero-medial and ventral surfaces of the mandible, and 3) a depressor mandibulae extending from the retroarticular process to the posterior and inner surface of the quadrate and quadratojugal. The latter origin is

improbable, of course, for such a location would have restricted or entirely obstructed the stapedial canal and tympanum. Lull also suggested that a masseter and buccinator may have been present—the former he placed between the coronoid process and the ventro-anterior margin of the jugal, the latter between the lateral ridges of the maxilla and dentary forming a short but broad cheek muscle along the full length of the dentition.

Russell (1935), in an analysis of *Chasmosaurus* featuring reconstructions of the neck, trunk and limb musculature as well as the cranial muscles, presented a reconstruction similar to that of Lull's with only minor differences in detail and terminology. He visualized a more prominent *M. temporalis* extending from the inner side of the coronoid process up through the supratemporal fossa and passing back to the caudal margin of the frill in *Chasmosaurus*. Russell considered this the principal adductor and, although his efforts were concerned chiefly with *Chasmosaurus*, he presented a similar interpretation for the temporal muscle in *Protoceratops*, *Styracosaurus*, *Centrosaurus (Monoclonius)* and *Anchiceratops*. Like Lull he restricted this muscle in *Triceratops* to that portion of the frill just posterior to the supratemporal fossa, believing that a defensive function had become dominant in the frill of this genus at the expense of the temporal muscles. Russell also represented the *M. pterygoidei* as attaching to the ventro-posterior surfaces of the mandible and the *M. massetericus* as extending from the medial surface of the jugal to the external surface of the coronoid process. He similarly followed Lull's interpretations regarding the buccinator and the *M. depressor mandibulae*, although he referred to the latter as the *Parieto-mandibularis* and suggested that its origin may have been situated further back on the underside of the frill near the extremity of the paroccipital process.

The most recent reconstruction of ceratopsian cranial musculature is that of Haas (1955) based on a number of skulls of *Protoceratops*. It is largely on Haas' interpretations that the following muscular reconstructions of *Triceratops* are based. Of these three studies, only Haas adhered to the typical sauropsid muscular pattern and terminology in considering the trigeminal musculature. Figure 6 illustrates the basic plan of the jaw musculature of *Protoceratops* as reconstructed by him.

As the present paper is concerned chiefly with the mechanics of mastication, only those muscles directly concerned with this activity are included in the following discussion. These include the various elements of the adductor mandibulae group of Luther (1914) and Lakjer (1926) (the *M. adductor mandibulae externus*, *M. adductor mandibulae internus* and *M. adductor mandibulae posterior*) and the *M. depressor mandibulae*, but exclude the other cranial muscles such as the constrictor dorsalis and constrictor ventralis groups. Since the ceratopsian skull was akinetic, the constrictor dorsalis, even if present, could not have contributed to mandibular adduction or mastication.

In accordance with Luther's work, the reptilian adductor mandibulae group is separable into three principal adductors—the external, internal and posterior, according to their positions with respect to the three branches of the trigeminal nerve. Haas has postulated a tripartite *M. adductor mandibulae externus* for *Protoceratops* originating on the upper surface of the parietosquamosal frill and the medial surface of the upper temporal arch, the fibers passing forward and downward through the supratemporal fossa to the mandible. The insertion he believed to have been in the mandibular fossa for the deeper fibers and along the crest and posterior border and lateral surface of the coronoid process for the more superficial fibers. This interpretation is supported by osteologic features of the *Protoceratops* skulls examined by Haas and by muscle patterns of certain modern sauropsids. But from a purely mechanical point of view, it would seem more probable that the bulk of the adductor externus fibers were applied against the dorsal extremity (rather than the base) of the prominent coronoid process. This most certainly was the point of attachment of the principal adductor in the higher ceratopsians with their much larger and higher coronoid processes and larger frills. A point of major significance is that Haas, like his predecessors, considered the frill as the enlarged platform of attachment for the principal jaw adductors—the *M. adductor mandibulae externus* (*M. temporalis* of Lull and Russell). The force of contraction of this large, complex muscle acting in the region of the coronoid was chiefly up and backward, a force vector oriented at approximately 60° to 70° back from the axis of the mandible.

Of the two portions of the adductor internus (*M. pseudotem-*

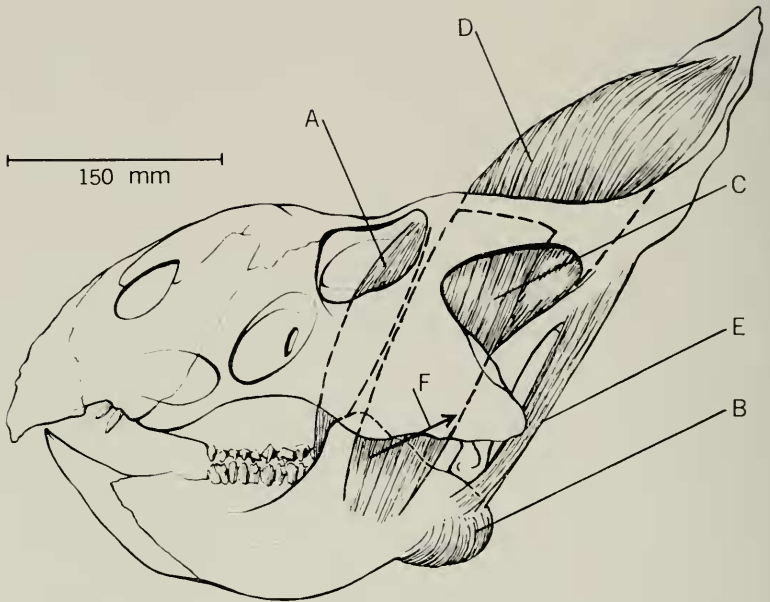


Fig. 6. *Protoceratops andrewsi* with the mandibular muscles reconstructed. Abbreviations: A, M. pseudotemporalis; B, M. pterygoideus; C, M. adductor mandibulae externus superficialis; D, M. adductor mandibulae externus medialis and profundus; E, M. depressor mandibulae; F, M. adductor mandibular posterior.

poralis and M. pterygoideus), Haas reconstructed the former as occupying a peculiar anterior position with the origin located in the orbital area and the fibers descending almost vertically to an insertion on the anterior slope of the coronoid process. Although the insertion is still open to question and may actually have been more intimately associated with the summit of the coronoid process, I am not able to support such a possibility with any concrete evidence for either *Protoceratops* or *Triceratops*. The strange orbital origin postulated by Haas is amply supported by good osteologic evidence, namely, the location of the trigeminal foramen, which is situated behind the pseudotemporalis in all living sauropsids. Contraction of the postulated pseudotemporalis would have produced strong vertical adductive forces. The second portion of the adductor internus, the M. pterygoideus, is reconstructed by Haas as a more complex muscle connecting the postero-lateral, ventral, and medial surfaces of the rear of the mandible with the

ectopterygoid—pterygoid process of the basi-cranium. This is consistent with the condition of modern sauropsids. With the rostral ascent of the pterygoideus fibers in *Protoceratops*, contraction would have produced a dorso-anteriorly directed adductive force. It is important to note that both adductor internus muscles (as reconstructed here for *Protoceratops*) are oriented at distinct angles to the other mandibular muscles and therefore would have generated adductive forces in directions quite different from those of the other jaw muscles.

The remaining trigeminal muscles, the *M. adductor mandibulae posterior*, is placed medial to the external adductors by Haas, extending from the anterior face of the quadrate to the splenial on the ventro-medial surface of the mandible and to the region immediately adjacent to and surrounding the entrance to the mandibular fossa. In my opinion this muscle probably accounted for the bulk of the muscular fibers that must have inserted in and around the Meckelian fossa, as in crocodylians and certain lacertilians, with the major part of the external adductors inserting more superficially on the upper extremities of the coronoid process. Contraction of the adductor posterior in this position would have produced a strong dorso-caudally oriented adductive force almost parallel to that generated by the more superficial adductor externus.

Although not a trigeminal muscle, the *M. depressor mandibulae* is intimately involved in jaw mechanics, as it is the sole mandibular diductor or depressor. Haas postulated this muscle as passing ventrally from the latero-ventral margin of the squamosal behind the quadrate to the medially expanded but caudally restricted retroarticular process. This position provides ample space for a superficial tympanum behind the quadrate, even though Haas suggests that the postquadratic region is perhaps too far distant from the fenestra ovalis to have permitted retention of a functional stapes and tympanum. In view of the extremely short postarticular length of the retroarticular process in *Protoceratops* (and in all higher ceratopsians, for that matter), and of the orientation of the proposed depressor fibers (a particularly critical point for higher ceratopsians), there is considerable doubt as to the functional value of this muscle. Whatever its position and orientation, it had

negligible leverage and consequently could not have been a significant factor in jaw depression.

The trigeminal musculature summarized below and illustrated diagrammatically in Figure 7 is reconstructed on the basis of 1) Haas' reconstructions for *Protoceratops*, 2) preservation of distinct muscle scars in one or more of the *Triceratops* skulls examined, 3) the spatial and mechanical requirements of the particular muscles, and 4) Luther's classification of sauropsid trigeminal musculature together with reference to the position of the trigeminal foramen.

Adductor internus group:

- M. pseudotemporalis (A): Origin in the posterior region of the orbit on the lateral surface of the laterosphenoid anterior to the trigeminal foramen. Insertion on the anterior expansion of the summit of the coronoid process.
- M. pterygoideus (B): Origin along the posterior surface of the ventral wing of the pterygoid and along the ventral margin of that process. Insertion on the ventrolateral, ventral and ventromedial surfaces of the rear of the mandible adjacent to the articulation.

Adductor externus group:

- M. adductor externus superficialis (C): Origin on the medial surface of the upper temporal arch. Insertion on or adjacent to the summit of the coronoid process.
- M. adductor externus medialis and profundus (D): Origin on the dorsal surface of the parietosquamosal frill adjacent to the supratemporal fenestra and possibly extending back to the frill margin. Insertion on the summit of the coronoid process.

Adductor posterior group:

- M. adductor posterior (F): Origin on the anterior face of the quadrate. Insertion along the margins and within Meckel's cavity.

Whether or not the precise locations and orientations here proposed for these muscles are accepted, several points must be emphasized. As illustrated in Figures 4 and 5, the available mandibular areas in *Triceratops* that could have served as sites of attachment for these muscles are much restricted. The two most obvious and likely sites are the coronoid process and the Meckelian fossa. Any muscle fibers that inserted in or near the latter almost certainly extended up and back, if not to the anterior surface of the quadrate (which shows distinct muscle scars), then higher

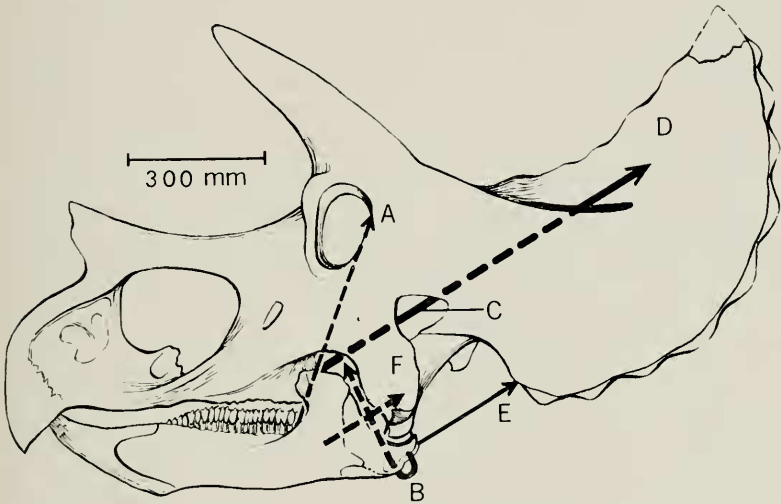


Fig. 7. *Triceratops brevicornus* with the location and action of the mandibular muscles indicated by arrows A — F. Abbreviations as in Fig. 6.

toward the supratemporal fenestra. There was no other place for these fibers. Those fibers that inserted along the summit of the coronoid process (attested to by very clear osteologic evidence) similarly could only have passed up and back. There was limited space behind the orbit, but the greatest portion of these fibers must have passed dorsocaudally to the supratemporal fenestra and beyond to the upper surface of the frill. There simply was no other space available to house these muscles within the temporal region of the *Triceratops* skull. Most significant of all, however, is the fact that the direction of action of these proposed "coronoid muscles" (the long arrow of Figure 7) is mechanically the most

effective line of action possible in a mechanical system such as that of *Triceratops*, in spite of the fact that this vector was not oriented perpendicular to the mandibular or lever axis. As the following discussion attempts to demonstrate, any other orientation of these "coronoid muscles" would have resulted in reduced leverage and thus lower adductive force.

MANDIBULAR MECHANICS

The vertebrate lower jaw during adduction operates as a third class lever (see Fig. 8) with the force (muscular contraction) applied at a point (or points) between the fulcrum (jaw articulation) and the resistance (dentition). As Davis (1955) noted, "this is a remarkably poor arrangement for masticatory purposes," for there is no mechanical advantage in a simple third class lever. The effective masticating force available at the dentition is less than the force of muscular contraction because the resistance lever arm (distance from the dentition to the articulation) is greater than the force lever arm (distance from the point of muscle attachment to the articulation). Force is sacrificed for a gain in speed of jaw adduction or displacement.¹

The collective effect of contraction of the mandibular adductor muscles is rotation of the mandible through a limited vertical arc about a horizontal transverse axis. Disregarding friction, the efficiency with which this rotation is accomplished is determined by the *moment arm* or leverage through which the adducting forces act. The moment arm, by definition, is the perpendicular distance between the line or direction of force action and the fulcrum. The force which can be exerted at any point along the dentition, then, is a function not only of the magnitude of the applied force, but of the lever or moment arm as well. The product of force and its moment arm length is termed the *moment* of that force.

In the simple third class lever of Figure 8A, the moment arm of the applied force is distance *b* and that of the resistant force is

¹ Displacement has generally been overlooked by most functional anatomists in their analyses of jaw mechanics, but obviously it is of considerable importance. Speed of adduction may be critical in predaceous vertebrates, but it cannot be considered important in herbivores. Gape of the mouth, however, is significant in both. Construction of the lower jaw as a third class lever permits maximum depression of the jaw with a minimum length of adductor muscle fibers.

distance $a + b$. Both moment arms are perpendicular to the line of action of the respective forces, which themselves (in this instance) are perpendicular to the lever axis. If the applied force, instead of acting perpendicularly to the lever, acts at some other angle, say 45° back toward the fulcrum (as in Figure 8B), the available force at any point along the lever will be less because the moment arm (or leverage) of the applied force is shorter. Distance b is no longer perpendicular to the line of force action and therefore is no longer the moment arm. The new moment arm, perpendicular to the new inclined force vector is b' and its length (and therefore the leverage of the applied force) is a function of the angle of inclination of the applied force (in this instance, 45°). The length of this moment arm then is the product of b and the \sin of 45° ($.7071b$).

Applying these mechanics to the vertebrate jaw, it would appear that the most effective mechanical arrangement is one in which the muscle fibers are oriented vertically, perpendicular to the jaw ramus and attached as far forward of the articulation as

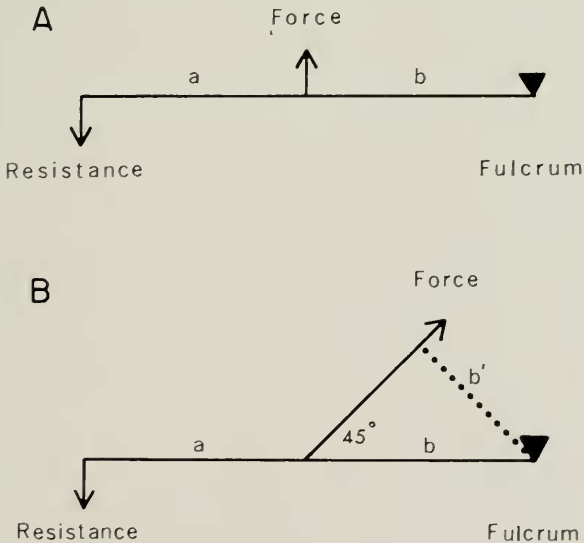


Fig. 8. Simple third class levers. A. Third class lever with parallel opposing forces. Moment arm of applied force equals b . Moment arm of resistant force equals $a + b$. B. Third class lever with nonparallel opposing forces. Moment arm of resistant force equals $a + b$. Moment arm of applied force equals b' .

possible. There are some obvious disadvantages in this arrangement, however, as has already been inferred. First, with the adductor muscles shifted forward away from the fulcrum, a corresponding reduction in possible jaw gape results. Second, the forward position of the adductor fibers would presumably restrict the size (and thus the power) of the jaw musculature, because the areas of origin would of necessity be concentrated in the facial region, beneath or in front of the orbits and along the snout.

The critical factor in a mechanical system of this type is the length of the moment arm (and ultimately the magnitude of the *moment* of the applied force). The effective force acting perpendicular to the structural member (jaw ramus) can *only* be magnified by 1) increasing the magnitude of the applied force or 2) lengthening the moment arm by shifting the point of force application *away* from the fulcrum. The first solution requires muscle enlargement and increased effort, whereas the second does not.

Where the applied force acts at some angle *other than* 90° to the structural member of the lever (as with the inclined force vector of Figure 8B), it is possible to increase the moment arm (and thus the effectiveness of the applied force) without shifting the point of force application along the jaw ramus away from the fulcrum (and thereby reducing the amount of gape possible). This can be accomplished simply by elevating the point of force application (muscle attachment) above the axis of the lever (as is achieved by the development of a coronoid process) or by depressing the fulcrum below the lever axis or both.

From these simple mechanics we may conclude that the development of a prominent coronoid process (as in *Triceratops*) or the depression of the jaw articulation (also as in *Triceratops*) results in an increase in the length of the moment arm of the principal mandibular adductors and therefore an increase in adductive force.

The ceratopsian mandibular lever is not a simple third class lever, but is one that has been modified in several ways. The principal differences are that the forces involved (resistant force between opposing dentitions and principal adductive force of muscular contractions) did not act in opposite directions, as in Figure 8A, but instead acted at a distinct angle to each other. Also, the three critical points of the ceratopsian lever (fulcrum,

point of action of the applied force, and point[s] of resistant action) did not lie on a simple straight axis. The fulcrum (articulation) lies well below the dentition or plane of resistant action and the principal point of force application (the coronoid process) is situated far above and lateral to the dental plane. The dentition, of course, marks the primary axis of the lever and those points at which the resistance acted.

The mandibular lever of *Triceratops* is illustrated in Figure 9 translated into diagrammatic terms. In this diagram, the combined lengths of the solid horizontal lines ($b + e' + a$) represent the total length of the mandible anterior to the center point of the jaw articulation (fulcrum). This distance is 76 cm in *Triceratops brevicornus* (YPM No. 1834). It represents the maximum moment arm of the resistant force. The double horizontal line ($e' + e''$) corresponds in length and position to the mandibular battery (37 cm long in *T. brevicornus*). The solid vertical line (h) represents the vertical distance from the top of the coronoid process to the level of the jaw articulation (17.5 cm in *T. brevicornus*) and its location corresponds to the position of the coronoid process along the mandibular ramus. The resistance (food), acting either at the beak or at any point along the dentition, is assumed to have acted perpendicularly to the jaw ramus. The applied force, however, (that generated by the dominant or principal adductor muscle—

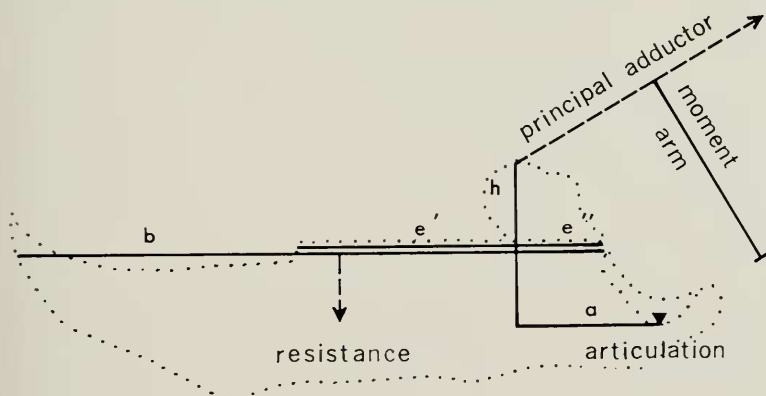


Fig. 9. Diagrammatic representation of the mandibular lever of *Triceratops*. Battery length equals $e' + e''$. Mandibular length equals $a + e' + b$. Moment arm of principal adductor as labeled (see b' of Fig. 8B). Moment arm of resistant force equals $a + e'$ (with the resistance placed as shown here). Height of coronoid process equals h .

M. adductor mandibulae externus) is interpreted as having acted along a line (long broken arrow of Figures 7 and 9) trending approximately 30° to 40° to the lever axis. This last interpretation, including the selection of the principal adductor, is based on the following assessment of the relative mechanical significance of the several mandibular adductors summarized on page 18 and in Figure 7.

- M. pseudotemporalis (A)—a minor adductor, probably of small size but with a long moment arm.
- M. pterygoideus (B)—a very minor adductor of moderate to possibly large size, but with a negligible or extremely short moment arm.
- M. adductor externus (C, D)—a very important adductor of large to very large size with a very long moment arm.
- M. adductor posterior (F)—probably a minor adductor of small to moderate size with a rather short moment arm.

As shown in Figure 7, the only mandibular muscles with moment arms of significant length, and therefore potentially dominant adductor muscles, were the pseudotemporalis (A) and the external adductor (C, D). Morphologic evidence indicates the latter to have been a very large muscle. No such evidence indicates a large size for the pseudotemporalis. The adductor externus, therefore, has been selected as the dominant *Triceratops* jaw muscle and the angle between its line of action and the dental row is angle θ , or approximately 30° in *Triceratops brevicornus* (see Fig. 10).

The length of the principal adductor moment arm of *Triceratops* cannot be measured directly with any accuracy when the lower jaw is in articulation and fully adducted (the critical position), but it can be calculated from other measurements taken from the skull and jaws (see Fig. 10). In *Triceratops*, the moment arm of the applied force is a function of the height (h) of the coronoid process above the level of the articulation, the lever distance (a) between the center of the articulation and the midpoint of the base of the coronoid shaft, and the attitude (angle θ)

of the line of action of the applied force (F) relative to the fulcrum. Angle θ can only be determined when the lower jaw is in the fully adducted position because 1) the line of action of the applied force relative to the mandibular lever is not constant but changes during elevation and depression of the jaw, and 2) we are concerned here only with the mechanical efficiency of the ceratopsian jaw in the act of shearing or masticating, and therefore in the occluded state. With the jaws fully adducted, a line passing from the summit of the coronoid process up and back through the supratemporal fenestra to the dorsal surface of the frill represents the line of action of the principal adductor—the adductor externus.

It is immediately apparent from the diagrams of Figures 7 and 9, that in spite of the close proximity of the jaw articulation and the coronoid process, the moment arm of the applied force (principal adductor) is very long. Consequently, we may conclude that the adductive efficiency of this part of the mandibular musculature of *Triceratops* was very high and presumably, that the masticatory powers were correspondingly great.

With these parameters, we can calculate the relative force that could be generated by the principal adductor at any point along the mandible of *Triceratops* as follows:

According to the laws of lever mechanics, rotation of the lever about the fulcrum can only occur when the lever is not in equilibrium. That is, when the moment of adduction or elevation exceeds the moment of depression, an elevating rotation of the jaw about the fulcrum will take place. When there is no resistance (food) between opposing dental batteries, the required adduction moment is small, just sufficient to overcome friction and the weight of the mandibles. When the dentition encounters resistance in the form of plant fibers to be cut or crushed, further rotation is accomplished only when the applied force exceeds the resistance of the food substance, or, in other words, when the moment of the applied force exceeds that of the resistance.

In Figure 10, the resistant moment is

$$S (e' + a)$$

where S equals the resistant force and $e' + a$ the moment arm of the resistance. The moment of the applied force is

$$F (m)$$

where F equals the applied force and m the moment arm of that force. Because m cannot be measured directly with any accuracy, it must be calculated:

$$m = \sin(\theta + \delta) d$$

where d represents the diagonal distance between the fulcrum and the point of muscle attachment at the summit of the coronoid process. (The diagonal d can either be measured directly or calculated by the Pythagorean theorem from h and a .) Angle δ is that between the diagonal and the lever axis.

From these we can calculate the usable force that could be generated at any point along the mandibular lever from:

$$S(e' + a) = F \sin(\theta + \delta) d$$

where e' equals any desired distance anterior to the coronoid process dependent upon the selected location of the food, and F is assumed to be unity or 100 per cent.

Substituting the appropriate values from *Triceratops brevicornus* (YPM No. 1834):

$$\begin{aligned} S(28 + 15) &= 100 \sin(30^\circ + 50^\circ) 23 \\ 43S &= 100 (.9848 \times 23) \\ 43S &= 2250 \\ S &= 52\% \end{aligned}$$

The selected distance for e' (28 cm) in the above calculation places the resistant force (food) at the anterior end of the man-

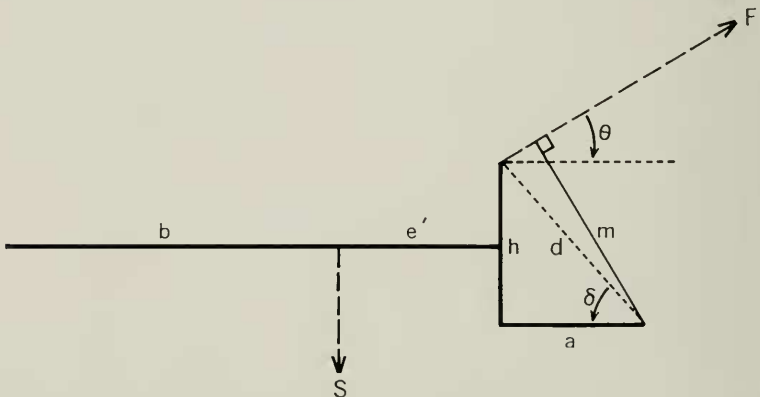


Fig. 10. Mechanical model of the mandibular lever of *Triceratops*, the basis of the accompanying calculations.

dibular battery. The calculations demonstrate that with the mechanical system described above for *Triceratops brevicornus*, one gram of occlusal force was available at the rostral extremity of the dentition for every two grams of contractile force exerted by the principal adductor.

TABLE I

Measurements of the Mandibular Lever of <i>Triceratops</i> (see Figures 9 and 10)	<i>Triceratops brevicornus</i> YPM No. 1834	<i>Triceratops elatus</i> AMNH No. 5116	<i>Triceratops elatus</i> USNM No. 2100	<i>Triceratops flabellatus</i> YPM No. 1821	<i>Triceratops prorsus</i> YPM No. 1822	<i>Triceratops serratus</i> AMNH No. 907	<i>Triceratops serratus</i> YPM No. 1823
Linear measurements in cm							
(a)							
Distance from the center of glenoid to center of coronoid process.	15.0	23.0	21.0	14.0	14.0	12.5	13.5
(h)							
Vertical height of coronoid process above glenoid.	17.5	22.0	24.0	19.0	17.5	22.0	17.0
(d)							
Diagonal distance from center of glenoid to crest of coronoid process.	23.0	31.5	32.0	23.5	22.5	27.5	21.5
(a + e' + b)							
Mandibular distance from center of glenoid to extremity of the beak.	76.0	102.0	88.0	82.0	75.0	90.0	72.0
(a + e')							
Mandibular distance from center of glenoid to rostral end of dentition.	43.0	68.0	58.0	46.0	45.0	55.0	42.0
(a - e'')							
Mandibular distance from center of glenoid to posterior end of dentition.	7.5	15.0	11.0	9.0	9.0	9.0	7.0
(e' + e'')							
Length of mandibular battery.	37.0	55.0	46.0	38.0	37.0	50.0	37.0
(θ)							
Attitude of principal adductor action relative to jaw axis.	30°	35	38°	35°	35°	30°	33°
(δ)							
Angle between jaw axis and diagonal (d).	50°	44°	49°	54°	51°	60°	52°

By the same procedure, the usable force at the beaks can be determined. Here the resistant moment arm is $a + e' + b$ (of Fig. 10) or 76 cm. The available force (S) at the beaks equals 29 per cent of the applied force or approximately one gram for every four grams of contractile force. This seems to be a rather low value, but when the total length of the mandible is considered, it is a remarkably high value, and it is consistent with the existence of the ceratopsian beak. It is highly unlikely that a specialized structure such as the ceratopsian beak would have been adaptive unless significant forces could have been generated between the beaks, but it is also clear that the beaks probably did not serve as an important shearing mechanism because of the great length of the mandibles and the correspondingly long resistant moment arm.

The full significance of the *Triceratops* mandibular lever is yet to be established. It is hardly necessary to point out that maximum occlusal forces are available at the rear of the vertebrate jaw, between opposing teeth closest to the fulcrum. But, in nearly all vertebrates, the available force at the rear of the tooth row is somewhat less than the total applied force. In *Triceratops*, however, this is not the case. As mentioned earlier, the mandibular battery extends far back in the jaw, almost to the articulation and well behind the coronoid process. The last tooth of the mandibular battery in *Triceratops brevicornus* (YPM No. 1834) is only 7.5 cm anterior to the center point of the jaw articulation. Thus, the resistant moment arm for the rear of the battery is

$$S \ 7.5 \text{ cm}$$

and the lever equation now becomes

$$7.5S = 100 \sin (30^\circ + 50^\circ) \ 23$$

$$7.5S = 2250$$

$$S = 300\%$$

At the caudal extremity of the batteries, an occlusal force of 3 grams is available for every one gram of contractile force applied to the mandibular lever by the principal adductor!

Similar analyses of the other six specimens of *Triceratops* produced essentially similar results. For all seven specimens, the adductive pressure that could have been generated at the beaks was approximately 30 per cent of the applied force (28% to

TABLE II

Mechanical Parameters of the Mandibular Lever of <i>Triceratops</i>	<i>Triceratops brevicornis</i> YPM No. 1834	<i>Triceratops elatus</i> AMNH No. 5116	<i>Triceratops elatus</i> USNM No. 2100	<i>Triceratops flabellatus</i> YPM No. 1821	<i>Triceratops prorsus</i> YPM No. 1822	<i>Triceratops serratus</i> AMNH No. 907	<i>Triceratops serratus</i> YPM No. 1823
Linear dimensions in cm							
(m)							
Calculated length of moment arm.	22.5	31.0	31.7	23.4	22.4	27.7	21.4
Moment arm as percentage of length of mandibular lever.	30%	30%	36%	29%	30%	31%	30%
Calculated force available at the beak as a percentage of force ap- plied by the principal adductor mus- cle.	29%	30%	36%	28%	30%	31%	30%
Calculated force available at the rostral end of the dentition as a percentage of force applied by the principal adductor muscle.	52%	45%	55%	51%	50%	50%	51%
Calculated force available at the caudal end of the dentition as a percentage of force applied by the principal adductor muscle.	300%	206%	288%	260%	250%	308%	305%

36%). The available force at the rostral extremity of the dentition approximated 50 per cent (45% to 55%) and at the caudal extremity of the dentition, the available shearing force ranged from 250 per cent to 300 per cent. The comparative mechanical efficiency of the mandibular lever of all seven specimens is summarized in Table II. Although differences do appear, there is remarkable consistency among the seven specimens for the several mechanical parameters calculated.

DISCUSSION

The most critical element in this analysis is the basis for the principal vector or assumed line of action of the applied force. This aspect of the problem may be approached in two ways: first, by calculating the average direction of adductor action (the combined action of all adductor muscles), or second, by determina-

tion of the probable line of action of the dominant or principal adductor muscle. The second approach was used in this analysis for several reasons. First, the combined effect of all the adductor muscles cannot be determined without some measure of the relative power of the respective muscles, even though their individual lines of action may be known. Any "average vector" calculated without these data would be highly subjective and speculative. Second, morphologic and mechanical evidence in both the skull and jaw clearly indicates that those muscles which occupied the "temporal" region in *Triceratops* were the dominant adductor muscles with the greatest bulk and the longest moment arm and therefore had the greatest impact on mandibular mechanics. Calculations based on such a dominant factor, although specifically applicable only to that solitary force, can be expected to approximate closely the combined effect of the total adductor complex.²

The summit of the coronoid process almost certainly served as the principal (if not exclusive) site of attachment of the adductor externus, but regardless of what specific muscle inserted here, that muscle must have been the most important of the jaw muscles. It had the longest possible moment arm and very probably the greatest bulk of any of the trigeminal muscles. The primary function of this muscle was adduction. The Meckelian fossa, by analogy with modern reptiles, probably represents the insertion area of the adductor posterior, which in *Triceratops* must have been a short, compact muscle originating on the anterior face of the quadrate and situated immediately adjacent to the jaw articulation. Although the adductor posterior may have been a powerful muscle, the very short moment arm indicates that it could not have been the dominant adductor muscle. The adductor posterior may well have served to prevent disarticulation of the mandibles as well as elevating the lower jaws. The fact that its orientation was almost parallel to that of the larger adductor externus suggests that its action would not significantly have altered the assumed actions of the above analysis. The moment arm, however, which was only one

² It is perhaps significant that when the vectors (the magnitudes of which are proportional to the respective moment arms rather than the unknown absolute power of the muscles) of each of the trigeminal muscles of *Triceratops* are added vectorally, the resultant vector orientation closely approaches (deviates by less than 10° in *T. brevicornus*) the direction of action reconstructed for the principal adductor.

third that of the adductor externus, means that this muscle had one third the adductive power of the adductor externus— *if* the two muscles were of equal size (an assumption deemed very doubtful in view of cranial evidence indicating the adductor posterior to have been much smaller than the adductor externus).

The position of the pseudotemporalis is not as certain as are those of the other adductors, but it is clear from cranial evidence that unless it occupied a most unlikely position, such as that postulated for the adductor externus (in which instance the above analysis would still apply), the pseudotemporalis could not have been a large muscle. In fact, it must have been a rather small muscle for there simply is insufficient space available within the anterior part of the temporal region of a *Triceratops* skull to house a large muscle. Regarding the pterygoideus muscle, the most probable position and orientation of these fibers (as shown in Figure 7) dictates that this muscle be disregarded as far as mechanics of adduction and mastication are concerned. Inserting on the ventral and medial (and probably also on the ventro-lateral) surfaces of the mandible immediately beneath and adjacent to the jaw articulation, its line of action passed virtually through the fulcrum and therefore its moment arm was of almost negligible length. Thus the adducting moment of the pterygoideus was very small regardless of how large a muscle it may have been. From its position and orientation, we may conclude that it served primarily to prevent disarticulation of the mandibles and with its sling-like form, passing beneath the rear of the mandible, counteracted the high stresses that must have occurred at the articulation during mastication.

The various linear dimensions included in the analyses presented here are perhaps the most reliable factors involved, in spite of the fact that the application of the applied force has been arbitrarily reduced to a point, just as the broad articular facet has been represented as a simple pivotal point. The greatest potential source of error lies not in the linear measurements but in the angular determinations. The attitude of the applied force relative to the lever axis is particularly critical and sensitive, for even very slight dorso-ventral crushing of the ceratopsian skull would result in a significant reduction of angle θ . Every effort was made to eliminate this source of error by ruling out any and all specimens distorted by post-mortem crushing. An indication of the degree

of success achieved in avoiding this source of error is reflected in the values obtained for θ . Among the seven specimens included in this report, the range of variation of θ was only 8 degrees (see Table I). We can assume, therefore, that the principal vector plotted for these calculations is dependable.

In spite of what may seem to be a gross over-simplification of a complex mechanical system (complex in the sense that several different vectors of unknown magnitude and uncertain orientation were responsible for the mechanical actions under consideration), it is believed that the analysis presented here contributes to our understanding of the functional significance of a highly specialized adaptation—the ceratopsian masticating apparatus. The values obtained for the relative adductive pressures at various points along the mandibular lever may not be precise, but they certainly represent reasonable approximations. More significant, however, they permit a quantitative assessment of the functional significance of particular component structures constituting this mechanical system, specifically, the precise role of the coronoid process, the significance of glenoid depression (or elevation), the importance of dental placement, and the attitude and construction of the suspensorium.

Two very important points stand out, as regards *Triceratops*. First, the shearing dentition, consisting of highly specialized dental magazines of great length located in the rear half of the jaws, functioned exclusively as shearing blades. Second, the great mechanical power of the mandibular lever, reflected in the massive jaw construction, the design of the articulation, the robust coronoid process, and the mechanical design of the mandibles, provided a very long moment arm relative to jaw length. To the latter must be added the enlarged mandibular musculature, indicated by the great dorso-caudal expansion of the parietosquamosal frill.

ECOLOGIC IMPLICATIONS

It is hazardous to speculate about such matters as ceratopsian food preferences, but the feeding apparatus of these animals, and that of *Triceratops* in particular, is so unusual that failure to at least consider these matters would be a serious lapse. The observations and interpretations presented here demand some response to

the obvious question—what did ceratopsians feed on that required such unusual dentures and powerful jaws?

It is quite evident that *Triceratops* species were highly specialized for feeding on specific and probably rather unusual plant foods. But what types of plants these might have been is not nearly so evident. The fact that shearing power has been so highly perfected at the complete expense of all crushing and grinding powers points to the exclusion from ceratopsian diets of any ordinary leafy plant tissues, fruits or seeds. The uniqueness of the dentition further suggests that ceratopsians probably were the only animals equipped to feed on these particular plants. The indications of great power in all ceratopsian mandibular systems lead to the conclusion that ceratopsian food was very tough and resistant.

Crushing or grinding are effective means of reducing most edible plant tissues to small, easily digested particles, but highly fibrous tissues are best cut or sliced. It therefore seems reasonable to suppose that ceratopsian food differed from more normal herbage by a highly fibrous texture. Of the plant varieties available during Late Cretaceous times, two seem to be reasonable candidates for ceratopsian feed — at least in terms of the resilient and highly fibrous character suggested. These are the cycads and palms. Both of these are characterized by numerous long, palm-like fronds that radiate out from the top of a simple, unbranched trunk. The fronds of living palms and cycads often are tough and highly fibrous and those known from Late Cretaceous sediments appear to have been of similar character. In most living and fossil cycads, and in some palms, the trunk is quite short, thus the fronds are close to the ground and well within the reach of “ceratopsian-sized” animals.

Whether or not either cycad or palm fronds could have provided sufficient nourishment for these Late Cretaceous dinosaurs is not known, but I know of no other plants from ceratopsian-bearing strata that possessed the physical characteristics suggested by ceratopsian dentitions.

SUMMARY

1. The dental batteries of *Triceratops* were elongated, highly specialized, continuous shearing blades completely devoid of all crushing or grinding capacities.

2. The mandibular lever was constructed for maximum mechanical efficiency and the highest adductive stresses through a) the lateral positioning, b) the prominent height, c) the robust construction of the coronoid process, d) the caudal expansion of the dentition, and e) the depression, inclination and buttressing of the glenoid facet, all of which contributed to either lengthening the effective moment arm of the applied force, or reducing that of the resistant force, or resisting the resulting high stresses at the articulation.

3. Adductive forces apparently were increased also by enlargement of certain mandibular muscles, this being reflected in the greatly expanded parietosquamosal frill and the prominent reinforcement and caudal inclination of the suspensorium.

4. Occlusal forces available at the beaks, and the rostral and caudal extremities of the dental batteries approximated 30%, 50% and 250% to 300% respectively of the force exerted by the principal adductor muscle. These are the result of the unusual mechanical construction of the mandible and of the dorso-caudal extension of the *Triceratops* skull.

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